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SOME NOTES ON TEMPERATURE
RELATIONS IN PLANT PHYSIOLOGICAL
PROCESSES

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INTRODUCTION

Two fields of research in plant physiology receive major attention in these years. First, the study of biochemical and biophysical processes within the plant cell, and, secondly, the study of ecosystems and their relations to the biosphere.

It seems good to evaluate what the position of the plant physiologist towards these two extreme fields of activities is and what sort of contributions he may attempt without necessarily being reduced to either an amateur biophysicist or biochemist or to an amateur ecologist.

A possible answer then may be that, on the one hand, he may aim at integrating the various reactions studied by biochemical and biophysical methods into the concept of the living cell as the smallest and fairly universal entity of independent life, and also with respect to its possibly specialized rôle in a multicellular organism. Looking at the other field, that of ecophysiology, he may aim at analyzing the rôle of the various plant components in their relationships to environmental factors, and, on the basis of this, try to contribute to the understanding of their relation to their neighbours (of the same or different species) in the vegetation.

Thus, towards the biochemical and biophysical problems the attitude of the plant physiologist may be primarily synthetic, to the ecological problems primarily analytical.

Ecophysiological developments in the last decade have laid strong emphasis

¹ Part of the data presented in this paper have been reported at the International meeting of the Society for Experimental Biology, Göteborg, July 1971 (1) and at a meeting of the Plant Physiological Section of the Royal Netherlands Botanical Society at Amsterdam, May 1972.

on collecting field data without much interference with the natural environment of the crop or the ecosystem. Computer facilities have enabled the research workers to evaluate the necessarily rather random data in terms of the multiple effects of separate environmental factors on the reactions of plants as they grow in the crop. This type of analysis requires sensible 'models' to be fed into the computer. These models try to make the most intelligent use of available physiological data. It lays at hand that the task of the ecologically minded plant physiologist in the first place will be to provide additional data and, especially, to stimulate analytical thinking about the obtained results, in order to evaluate their trends and 'band width' with respect to naturally occurring variation in environmental conditions.

With this in mind, it seems appropriate to consider reactions of plants to temperature which is one of the major environmental factors controlling growth and development of plants in the temperate regions. Thus, in the present paper I have tried to summarize some basic features of reactions of plants to temperature which result from interactions between various processes in the living cell, and from correlations between different plant organs. The realisation of some of these background phenomena may contribute to render simulation models more realistic and increase the awareness of the boundaries of their validity.

The following subjects will be briefly discussed:

- 1) the linear temperature relationship,
- 2) the negative temperature relationship,
- 3) the significance of temperature sums (or heat sums).

1. THE LINEAR TEMPERATURE RELATIONSHIP

It is well-known that the temperature dependency of plant physiological processes often is linear. Data showing this are already present in literature earlier than 1930, and later some more examples have been found.

Only in few cases attempts have so far been made to explain the linearity, which, usually, was denoted as 'simple'. This simplicity, however, can only be apparent, if one realizes that, according to the VAN 'T HOFF-ARRHENIUS law, rather an exponential relationship should be expected showing constant proportions between the rates of a process at intervals of, e.g., successive temperatures which are 5° or 10° apart. It is easy to see that a linear relationship does not fulfill this requirement. On the contrary, the Q_5 -value will decrease in successive temperature intervals and, dependent on the precise shape of the temperature relationship, decrease more inasmuch as the temperature rises (figure 1). This figure is theoretically constructed for a case with a linear course of the temperature curve above 3 different temperature values. The concomittant Q_5 -values for the various temperature intervals are represented in the figure.

The figures 2, 3, 4, 5, and 6 (cf. ref^s. 2-6) show this course of Q_5 for some temperature curves from literature with more or less pronounced linear parts. In the case of figure 6 (respiration of *Phycomyces*), the data proved to be liable to a

FIG. 1. A theoretical example of a temperature curve of a metabolic process with deviations from exponentiality and their influence upon Q_5 -values in ranges of increasing temperatures. ● Rate values, × Q_5 -values. *Exp*: an exponential relation with $Q_5 = 1.6$ (cf. horizontal Q_5 -line, marked *Exp*). A, B, C: curves deviating from *Exp* to linearly respectively at 10°, 15°, and 20°C (●), and the corresponding Q_5 -values (×) for the successive temperature ranges. No attempts have as yet been made to 'understand' the exact course of the Q_5 -curves.

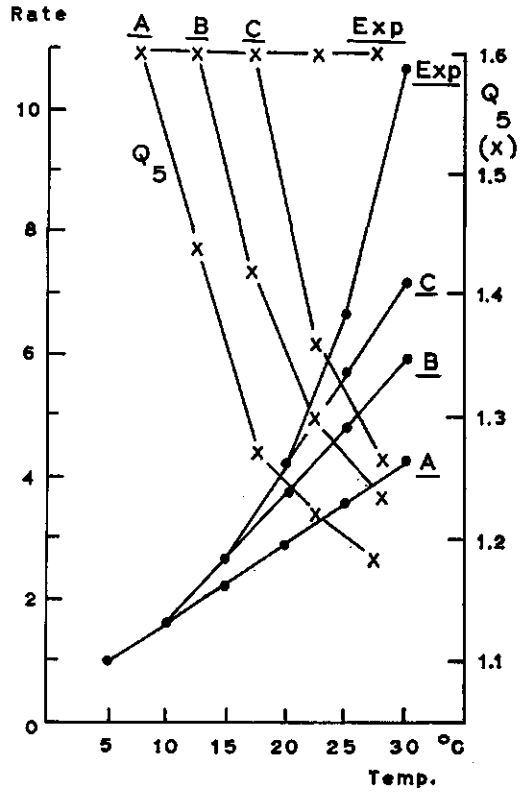
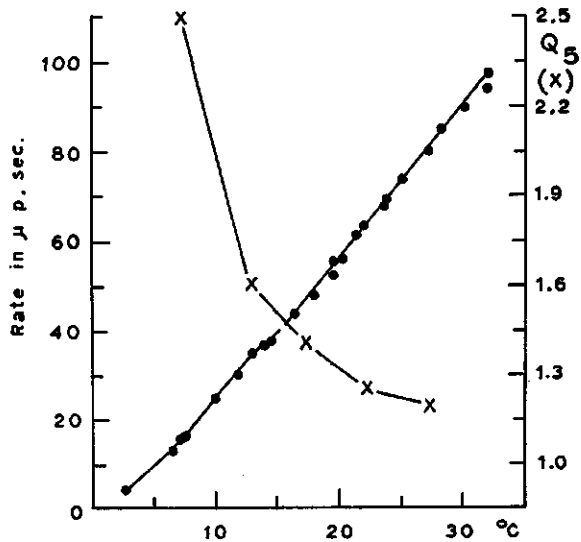


FIG. 2. Temperature curves of protoplasmic streaming in *Chara foetida* (adapted from ref. 2), and the course of Q_5 -values (×, added).



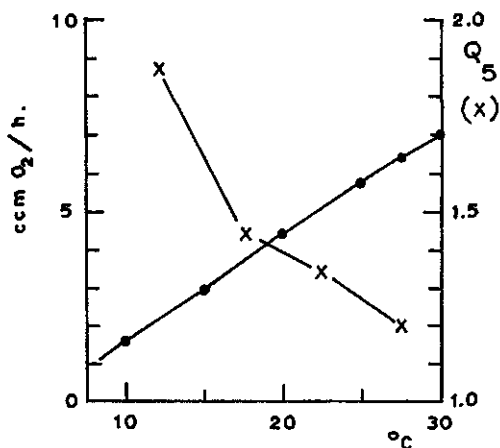


FIG. 3. Temperature curve of respiration (O₂-consumption) of *Phycomyces* on bread (●) (adapted from ref. 3), and the corresponding Q₅-values (×, added).

FIG. 4. Temperature curve of respiration of the root system of a corn plant (*Zea Mais* L.) raised at 25°C (○, from ref. 4), and the corresponding Q₅-values up to 30°C (×, added).

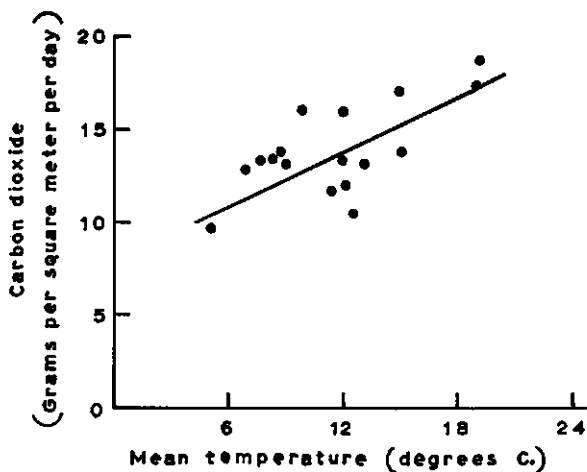
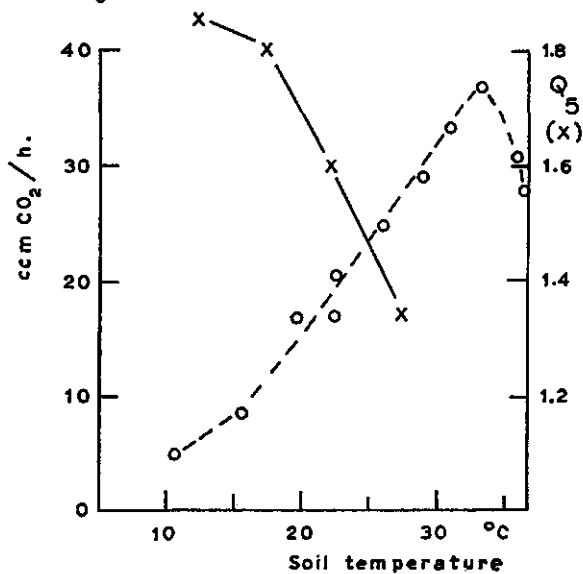


FIG. 5. Respiration rates of a forest (●) in summer against mean temperature (adapted from ref. 5); the straight line through the points was drawn by the author of the article (5). $Q_{10}^0/5^0 = 1.24$, $Q_{15}^0/10^0 = 1.20$, $Q_{20}^0/15^0 = 1.16$.

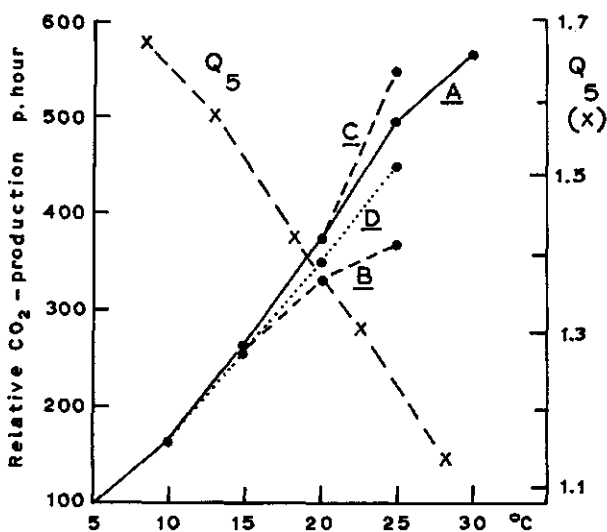


FIG. 6. Respiration versus temperature curves of *Phycomyces* on glucose media. Curve A was constructed by putting the value at 5° equal to 100, those for the higher temperatures were calculated with the aid of the Q_5 -values determined (averages of several data). The other curves were linked with curve A at the lowest temperature recorded in each case (adapted from ref. 6). The curve representing the Q_5 -values for curve A (x) was added for the purpose of this article.

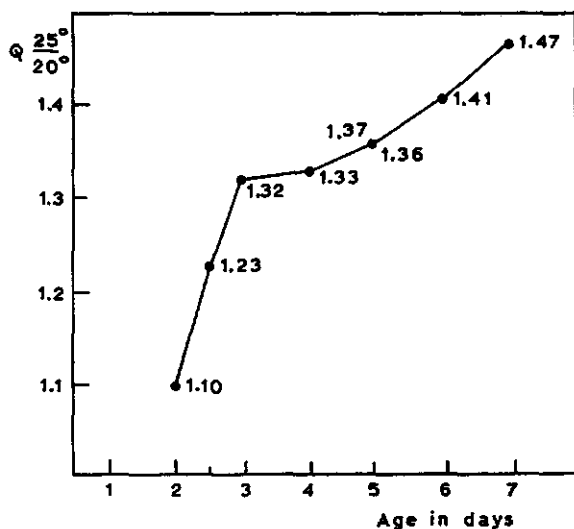


FIG. 7. Respiration of *Phycomyces* on glucose media. Change of $Q_{25/20}$ with age in days of the culture. Cultures on 4% glucose (adapted from ref. 6).

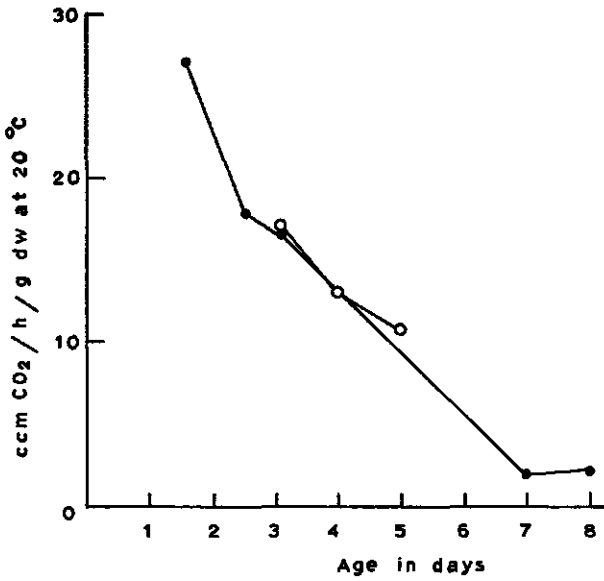


FIG. 8. Respiration of *Phycomyces* on glucose media. Respiration rate per unit dry weight in relation to the age of the culture (adapted from ref. 6).

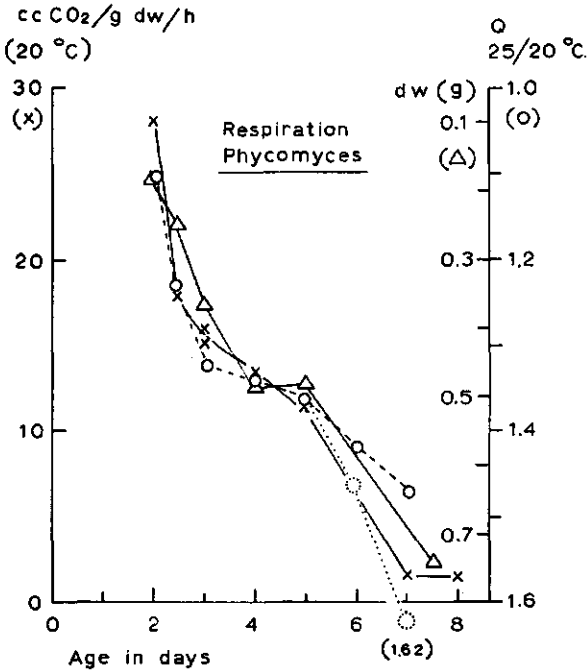


FIG. 9. Respiration of *Phycomyces* on glucose media. Linear correlation between the rate of respiration (x), dry weight of the culture (Δ) and the value of $Q_{25^{\circ}/20^{\circ}}$ (O) in relation to age (original, data from ref. 6).

beginning of an analysis since it was found that, especially in the temperature range from 20°–25°C, the Q_5 -value depends strongly on the age of the culture. The Q_5 -values for this temperature range was higher the older the culture was (6).

Figure 7 shows this very clearly, in which $Q_{25^\circ/20^\circ}$ is plotted against the age of the culture. Figure 8 shows the relation between the absolute values of the respiration rate, per unit dry weight, and the age of the culture. Finally, figure 9 shows the relation between $Q_{25^\circ/20^\circ}$, the respiration rate per unit dry weight, and the total dry weight of the culture. Using an adequate choice of the ordinate values, a very clear correlation between these sets of data becomes apparent. Most relevant, probably, is the relation between $Q_{25^\circ/20^\circ}$ and the respiratory rate. In young cultures, with the highest intensity of respiration, $Q_{25^\circ/20^\circ}$ is lowest; the most probable explanation herefor seems to be that, at high respiration rates, rate limitation is performed by a mass flow or diffusion process of a respiratory substrate, yielding low Q_5 -values. The most probable substance introducing this limitation seems to be the glucose content of the culture solution. Indeed, it was found that increase of the glucose concentration¹ from 4% to 15% in young cultures increased the values of $Q_{25^\circ/20^\circ}$. In very old cultures the respiration intensity appears to be so low that curtailing of respiration by substrate supply does not easily occur, explaining the higher $Q_{25^\circ/20^\circ}$ values (6).

According to this explanation, one may assume that a linear temperature relationship arises because, with increasing temperature, the measured rate of a metabolic process is increasingly curtailed by a reaction with low Q_5 -values, probably in many cases a mass-flow or diffusion process.

In the case discussed, the most probable factor limiting by diffusion was glucose. Whether also limited oxygen supply may have played a rôle was so far not investigated in this case, the possibility herefor may exist; however, during the experiments, the cultures were rocked.

In the same period, BOTTELIER (7) showed that the linear temperature relationship of protoplasmic streaming in *Avena* coleoptiles was age-bound as well, and in the same sense as was demonstrated above for the respiration of *Phycomyces*. Low Q_5 -values predominated in a larger range of temperatures inasmuch as the plants were younger. With this material a very nice set of data was obtained (figure 10). Under the experimental conditions chosen, limited oxygen supply was demonstrated to cause the low Q_5 -values in the higher temperature range in young plants. Mechanism and background of the protoplasmic streaming still are not very well understood but it lays at hand to suppose that respiration provides the necessary energy, possibly as ATP; renewed investigation of the detailed relation of the rates of respiration and of protoplasmic streaming, and connection with membrane physiology, would appear promising.

¹ The *Phycomyces* cultures for these experiments were grown on a synthetic medium with glucose as an energy source, the obligatory inorganic salts, and a small quantity of purified yeast extract for vitamin requirements (see ref. 6), and a neutral solid substrate (gravel).

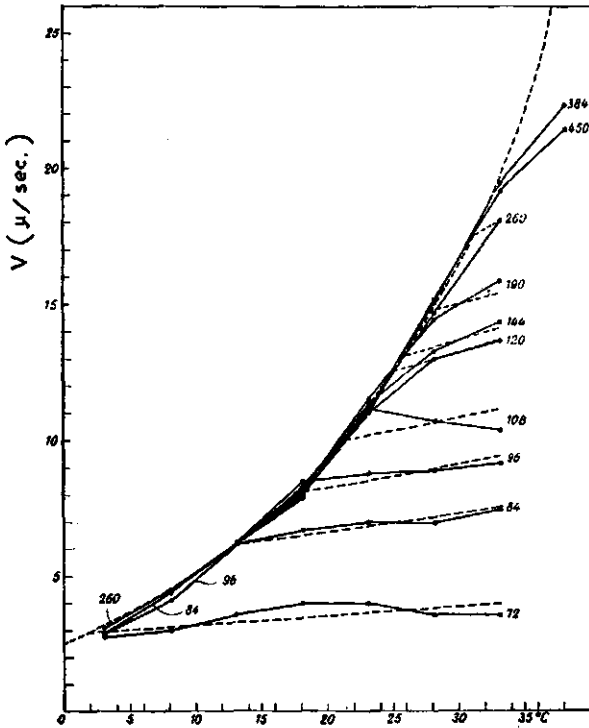


FIG. 10. Protoplasmic streaming in *Avena*-coleoptiles. Influence of temperature on the rate of protoplasmic streaming in relation to age of the plantules (adapted from ref. 7).

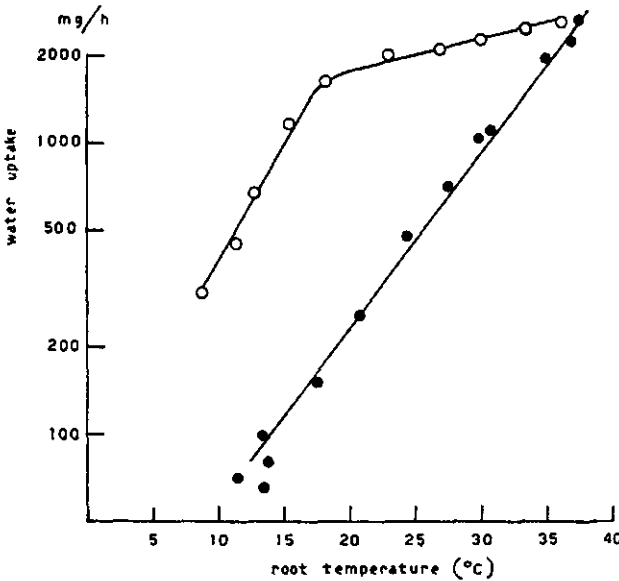


FIG. 11. Water uptake by intact bean plants grown in strong light. Effect of the temperature on water uptake of roots of plants grown at 17°C (○) and grown at 24°C (●) (log. scale, from ref. 8).

Fairly recent work by P. J. C. KUIPER (8) showed that the temperature relationship of water permeability in bean roots (*Phaseolus*) has a low temperature range with high or even extremely high Q_5 -values, and a high temperature range with low Q_5 -values. Interestingly, the transition between the two ranges depended upon the temperature at which the seedlings were raised (figure 11). In the range of low Q_5 -values, water permeability is probably governed by the viscosity of water, the high Q_5 -values in the lower temperature range reflect changes in membrane permeability which in part are probably of a structural nature ('statistic pores').

A particularly interesting case is that represented in figure 5 since it is concerned with the respiration/temperature relation of an entire ecosystem. The flat slope of the line and the low Q_5 -values suggest that mass-flow processes (availability of respirable substrates?) play a predominant rôle throughout the whole temperature range. More cannot be said without a detailed further experimental analysis.

2. NEGATIVE TEMPERATURE RELATIONSHIPS

These comprise some cases in which the measured rate of a process decreases with increase in temperature, viz., $Q_5 < 1.0$. The few cases in which a closer understanding has been attempted can be explained without assuming negative temperature coefficients in single parts of the process, but can be understood from interactions between elementary processes or from correlations between different plant organs. A classical example of negative temperature relationships is starch hydrolysis in plant organs. It is well-known from potato tubers, but can also be demonstrated in leaf discs, e.g. in *Helianthus* species. In leaf discs from

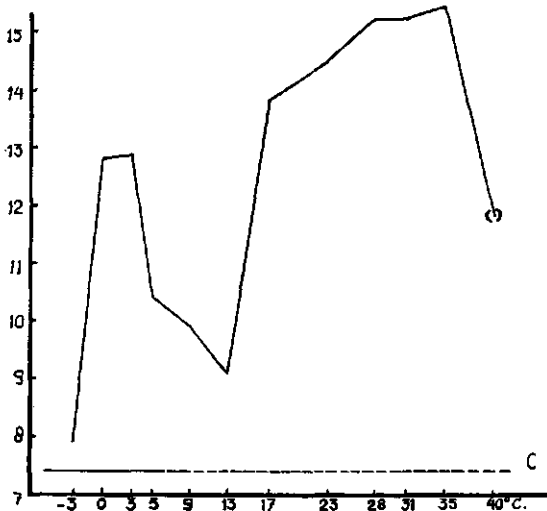


FIG. 12. Starch hydrolysis in leaf discs of *Helianthus annuus* in relation to temperature. Exposition time 14½ hours. Averages of 6 leaves. C = initial value (from ref. 9).

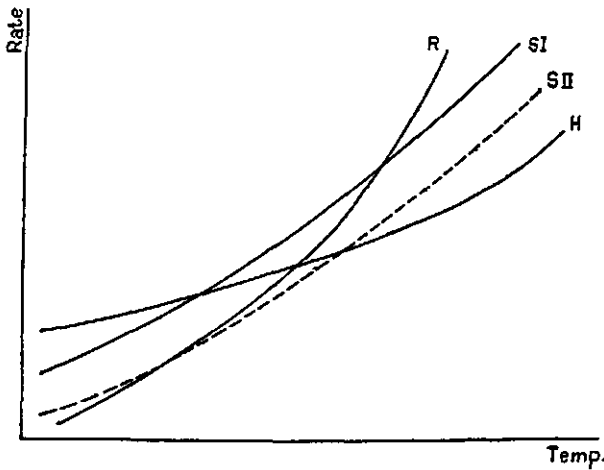


FIG. 13. Starch hydrolysis in *Helianthus* leaves. Scheme representing possible increments of starch hydrolysis (H), (re)synthesis of starch (SI and SII) and respiration rate (R). In the position SI synthesis would outdo effects of hydrolysis and respiration in the middle of the temperature region (from ref. 9).

sunflower and topinambour a maximum of starch hydrolysis appears at 3°C, a pronounced minimum at about 10°C, and a renewed increase at still higher temperatures (9). Thus, in the region between 3° and 10°C, a negative temperature relationship prevails (figure 12). In figure 13, an attempt is illustrated how the behaviour described might be understood on the basis of positive temperature relationships alone, be it with different Q_{10} -values. Attempts to substantiate this explanation in leaf discs of *Helianthus* were unsuccessful: resynthesis could not be demonstrated. There are, however, reports that in stems of *Acer* species

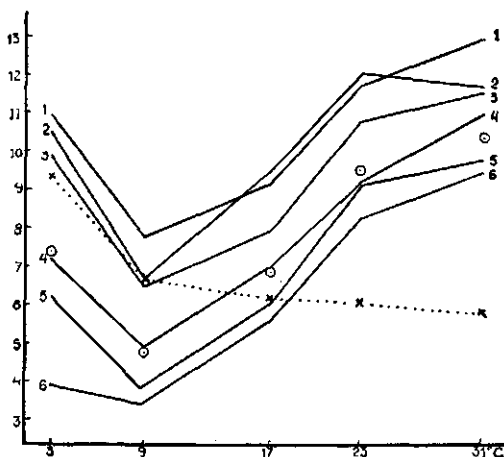


FIG. 14. Starch hydrolysis in *Helianthus* leaves in relation to temperature. Effects of age of the leaves (increasing from 1-6) of *Helianthus tuberosus* on starch hydrolysis, showing decrease of 3°C-value especially in stage 6. (adapted from ref. 9, see further legend of the original figure).

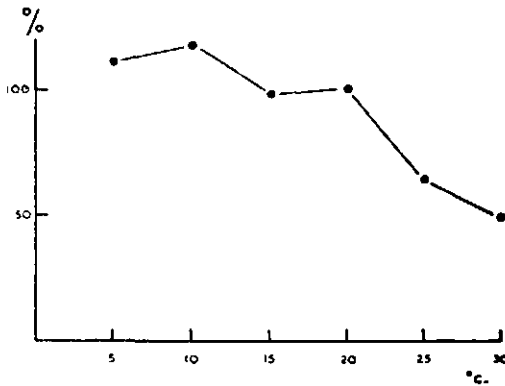


FIG. 15. Root elongation in *Acer saccharinum* seedlings. Relation of root elongation to shoot night temperature. Roots at 20°C (from ref. 10).

in Canada, resynthesis of starch occurs after strong cooling during the night, increasing the sugar content, and exposure of the stems to sunlight in the morning. It may be mentioned in addition that certain data obtained with *Helianthus* contain evidence that the peak of hydrolysis at 3°C is rather independent of the behaviour at higher temperatures: inasmuch as the leaf was older, the peak at 3°C was smaller (figure 14).

A second example of a negative temperature relationship was found in root-growth of *Acer spec.* (RICHARDSON,¹⁰) in relation to the night temperature of the shoot in the region from 5° to 30°C; the roots were all kept at 20°C (figure 15). The reason for the negative temperature relation probably is that increased shoot temperature during the night claims more of the products of photosynthesis, and leaves less for the roots, thus, a correlative effect.

At various root temperatures, and a shoot temperature of 20°C, there was a negative temperature relationship for root growth above 20°C (figure 16). In this case the explanation probably is that the increased requirement of the roots

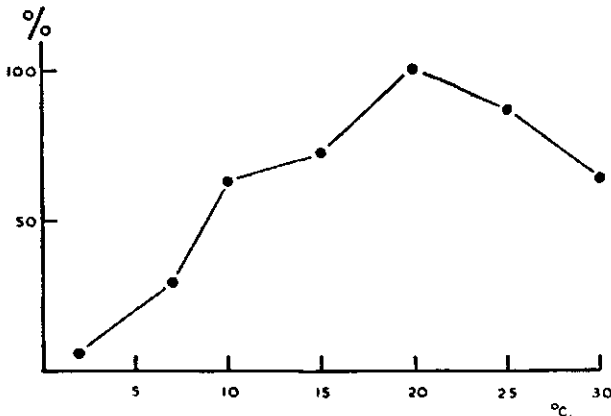


FIG. 16. Root elongation in *Acer saccharinum*. Relation between root elongation rate and root temperature. Shoots at 20°C (from ref. 10).

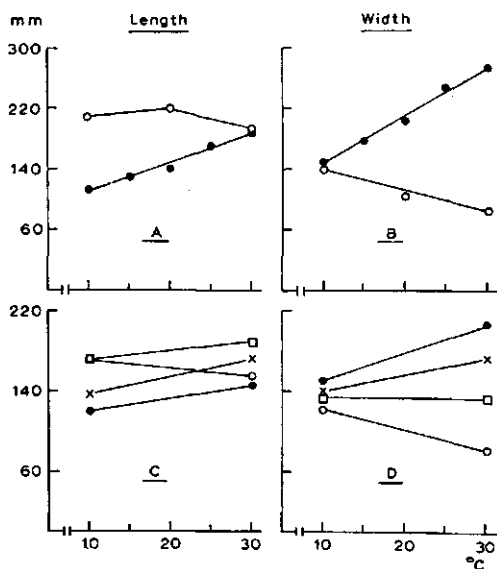


FIG. 17. Leaf shape in lettuce. Maximum leaf length (A and C) and maximum leaf width (B and D) in relation to temperature, at different light intensities. A and B: ca. 10,000 ergs/cm² sec (○); ca. 80,000 ergs/cm² sec (●), C and D: same as A and B, and additionally 25,000 ergs/cm² sec (□), 55,000 ergs/cm² sec (×) (from ref. 11, only leaf width is discussed in the present paper).

for assimilates cannot be fulfilled by the shoot, kept at a relatively lower temperature. This effect may still be enhanced by the higher rates of dissimilation in the roots themselves at the higher temperatures.

As a third example of a negative temperature relationship we mention that described by BENSINK (11), viz., the decreasing leaf width in lettuce in the temperature range of 10° to 30°C at low light intensities. Conversely, at high light intensities, the relation is positive, and there is a smooth transition between both types of relation at intermediate light intensities (figure 17). Moreover, both types of relation appear linear against temperature which will not be discussed here since the background is not yet sufficiently explored.

A fact of importance appears to be that the rate of leaf production increases with temperature at all light intensities (figure 18). In relation to this fact it is plausible to ascribe the decrease in leaf width with increasing temperature at low light intensities to an increased competition between successive leaves for available substrates. It seems that, at high light intensity, sufficient energy is available to increase the growth of each leaf with temperature, notwithstanding the fact that leaf number increases as well (consult further ref. 11).

Experiments with removal of the tip in sunflower at an advanced stage of growth (12) have shown that leaves below the decapitation point become larger than in untreated control plants; there are indications that also their sugar content increases. Some cases of similar behaviour have been reported in literature.

Data of BENSINK (11) also showed that cell number, at low light intensity as compared with high light intensity, is more reduced at 30°C than at 10°C, while cell size is smaller as well. On the whole, leaf width in lettuce shows a stronger correlation with cell number than with cell size (i.e., section 4.4., point 6).

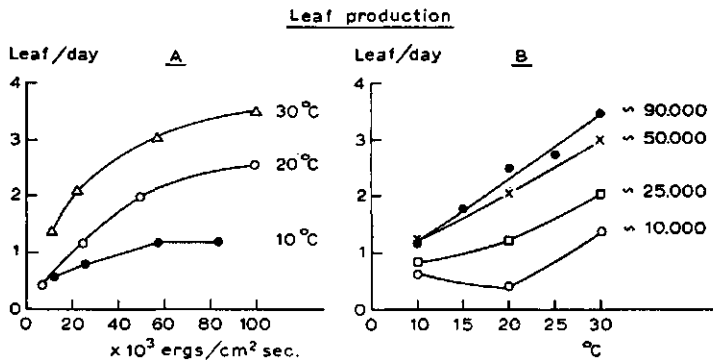


FIG. 18. Leaf production in lettuce. Numbers of leaves produced per day in relation to light intensity and temperature (from ref. 11).

Additional data of BENSINK (l.c.), and unpublished experiments of the effect of gibberellin on leaf development by VAN DER MEER suggest that growth of individual plant organs is the result of a delicate balance between energetic effects and formative effects and that various types of changes in the environmental conditions influence this balance.

Temperature studies as described here may give information about factors which determine the above balance and are at the base of morphogenetic reactions which affect size and shape of a plant and its separate organs, and their mutual proportions (e.g. length/width relations in leaves, top/root relationship, formation and filling of reserve organs, and others).

3. TEMPERATURE SUMS

The contention of temperature sums or heat sums goes back into the 19th century, and probably still further. It says that growth of plants and certain developmental phenomena are governed by the total amount of heat a plant received during a certain period. Originally, the average daily values of the temperature in degrees centigrade were counted up during a certain period. Later on, certain 'refinements' have been proposed by starting from minima, differing from 0°C. The reliability of the concept has been extensively discussed in terms of *pro* and *contra*. Details of its history cannot be discussed here (cf. also ref. 13). One may say that the concept received support from those phenological observations that indicate that the earliness of plant and animal development in spring is primarily determined by the average temperature in the preceding period. Figure 19 shows that different phenomena show corresponding peaks of earliness or lateness which were in accordance with the meteorological earliness or lateness of the entrance of spring, i.e. with the average temperature in the preceding period.

In connection with the discussion in the present paper, one may state that a

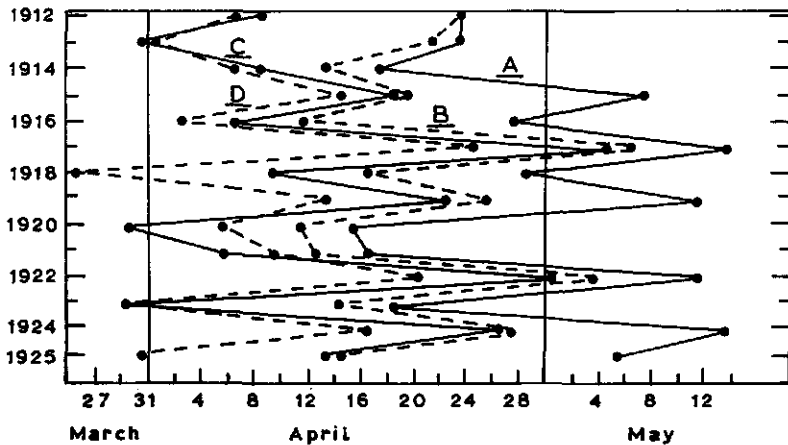


FIG. 19. Phenological data in relation to spring time in different years. Dates, at Wageningen, of first observation of leaves in *Aesculus hippocastanum* L. (A), first appearance of flowers in *Pirus malus* L. (C), and first observation of egg-laying of *Parus cristatus mitratus* BREHM (B) and of *Parus coeruleus coeruleus* L. (D), in the years 1912–1925 included. Full-drawn lines: the botanical observations, dotted lines: the zoological ones (adapted from ref. 14).

correlation between the rates of growth and development, and temperature sums may be expected in cases in which temperature is relatively low so that strongly temperature dependent processes determine the overall picture. According to section 1 of this paper, this will be primarily so at low temperatures. When the overall picture is predominantly determined by processes with low Q_{10} -values (photochemical processes, mass-flow processes, etc.) no clear correlation with the average environment temperature can be expected. This will be so as soon as the average temperature is sufficiently high to allow high rates of enzymatic processes. It explains why phenological observations in spring correlate much better with temperature sums than those on phenomena occurring in summer (e.g. harvest data).

Phenological observations appear to be somewhat out of fashion. However, they may be able, in the course of years, to provide useful indications on smooth changes in the environment, e.g. thermic pollution. Additionally, they may also give evidence about possible changes in temperature dependency of metabolic processes as a consequence of their being affected by sources of air and water pollution.

4. SUMMARY

The preceding sections may have shown that temperature relationships of metabolic processes are by no means fixed but may be influenced among others by the following factors:

1. Cooperation between partial processes with widely different Q_5 -values.

2. Interaction between processes that go in different directions, e.g. hydrolysis and synthesis, synthesis and respiration, etc.
3. Effects of competition between various plant organs (correlative effects).
4. The possibility plants seem to have to react in an additive way on successively administered amounts of heat over a longer period.

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